

Marmota caligata (Rodentia: Sciuridae)

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Abstract: *Marmota caligata* (Eschscholtz, 1829), a large ground squirrel commonly called the hoary marmot, is 1 of 15 species of extant marmots. It is distributed in western North America from Alaska and Canada south to Washington and Montana and is found at elevations ranging from sea level to 2,500 m. *M. caligata* prefers alpine and subalpine boulder piles and talus slopes surrounded by meadows. The species is listed as “Least Concern” by the International Union for Conservation of Nature and Natural Resources, although populations of Montague Island and Glacier Bay are of conservation concern by the State of Alaska.

Key words: Canada, hoary marmot, marmot, North America, Sciuridae, United States

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Marmota caligata (Eschscholtz, 1829) Hoary Marmot

Arctomys pruinosus Richardson, 1828:518. Not *Arctomys pruinosus* Gmelin, 1788.

Arctomys caligata Eschscholtz, 1829:1, pl. 6. Type locality “in nördlichsten Theile der Westküste Amerika’s, häufig an der Bristolbai [in the northern areas of the west coast of America, frequently on Bristol Bay];” restricted to “near Bristol Bay,” Dillingham County, Alaska by J. A. Allen (1877:927).

Arctomys? pruinosus Richardson, 1829:150. Not *Arctomys pruinosus* Gmelin, 1788.

arctomys Okanaganus King, 1836:236. Type locality (p. 241) “In a small tract of country, on the borders of the Rocky Mountains, lying between the Columbia and Fraser’s Rivers;” restricted to the “Gold Range, British Columbia,” Canada by Howell (1914:17).

arctomys okanaganii King, 1836:unnumbered pl. Incorrect subsequent spelling of *Arctomys okanaganus* King, 1836.

Arctomys pruinosus Audubon and Bachman, 1854:17, pl. CIII. Not *Arctomys pruinosus* Gmelin, 1788.

Arctomys caligatus Tyrrell, 1888:88. Correction of gender agreement.

Marmotta caligata J. A. Allen, 1903:539. Unavailable genus name (International Commission on Zoological Nomenclature 1954, Opinion 257).

Marmota caligata: MacFarlane, 1905:751. First use of current name combination.

Marmota vigilis Heller, 1909:248. Type locality “from west shore of Glacier Bay [Coppermine Cove], [Hoonah-

Angoon County], Alaska.” “Coppermine Cove” is given in the description of localities (Stephens and Dixon 1909:178) and the Museum of Vertebrate Zoology collection database.

Marmota sibila Hollister, 1912:1. Type locality “from head of Moose Pass branch of the Smoky River, Alberta; 7,200 feet,” Canada; preoccupied by *Arctomys sibila* Wolf, 1808.

[*Marmota*] *okanaganus*: Howell, 1914:17. Name combination.

Marmota caligata cascadiensis Howell, 1914:17. Type locality “Mt. Ranier, [Pierce County] Washington (altitude 6000 feet).”



Fig. 1.—An adult *Marmota caligata* from Highwood Pass, Alberta Province, Canada. Image 427 of the Mammal Image Library. Used with permission of the photographer J. O. Murie.

Marmota caligata nivaria Howell, 1914:17. Type locality “from mountains near Upper St. Mary’s Lake, [Glacier County], Montana (altitude about 6100 feet).”

Marmota caligata sheldoni Howell, 1914:18. Type locality “Montague Island, [Valdez-Cordova County], Alaska.” “Montague Island, Zaikof Bay” is given as the locality in the United States National Museum collection database.

Marmota oxytona Hollister, 1914:251. Replacement name for *Marmota sibila* Hollister, 1912, preoccupied by *Arctomys sibila* Wolf, 1808.

Marmota caligata raceyi Anderson, 1932:112. Type locality “Itcha mountains, Chilcotin plateau, range 3, Coast district, latitude 52° 45′ north, longitude 125° west; altitude 6,500 feet,” British Columbia, Canada.

Marmota marmota caligata: Rausch, 1953:120. Name combination.

Marmota marmota cascadenis: Rausch, 1953:120. Name combination.

Marmota marmota nivaria: Rausch, 1953:120. Name combination.

Marmota marmota okanagana: Rausch, 1953:120. Name combination.

Marmota marmota oxytona: Rausch, 1953:120. Name combination.

Marmota marmota raceyi: Rausch, 1953:120. Name combination.

Marmota marmota sheldoni: Rausch, 1953:120. Name combination.

Marmota marmota vigilis: Rausch, 1953:120. Name combination.

CONTEXT AND CONTENT. Order Rodentia, suborder Sciuromorpha, family Sciuridae, subfamily Xerinae, tribe Marmotini, genus *Marmota*, subgenus *Petromarmota*. Three subspecies are recognized (Thorington and Hoffmann 2005):

M. c. caligata (Eschscholtz, 1829:1, pl. 6). See above; *sheldoni* Howell and *vigilis* Heller are synonyms.

M. c. cascadenis Howell, 1914:17. See above; *raceyi* Anderson is a synonym.

M. c. okanagana (King, 1836:236). See above; *nivaria* Howell, *oxytona* Hollister, and *sibila* Hollister are synonyms.

NOMENCLATURAL NOTES. Allen (1902:17, 1903:539) proposed the use of the genus name *Marmotta* following von Zimmermann (1777:509). However, von Zimmermann’s (1777) *Specimen Zoologiae Geographicae* was rejected “for nomenclatural purposes because the author did not apply the principles of binomial nomenclature” (International Commission on Zoological Nomenclature 1954:233); *Marmota* Blumenbach (1779) retains priority. Gmelin (1788) proposed the name *Arctomys pruinosus* on the basis of the hoary marmot of Pennant (1781). Pennant (1784) later indicated that the

specimen was deposited in the Leverian Museum; however, the specimen is purported to be lost as it was sold when the Leverian Museum was dispersed by lots at auction in 1806 (e.g., Sabine 1822). Although King (1836:236) and others clearly recognized that the name *Arctomys pruinosus* Gmelin was not applicable to the hoary marmot, the name continued in use until Tyrrell (1888:88), in a comparison of Pennant’s description with specimens of some of the American species, concluded that it was unidentifiable and the name *pruinosa* was rejected (see also Howell 1915:59).

Type specimens for taxa given above (except *caligata*, which could not be determined or is not known to exist) are present in the collections at the Canadian Museum of Nature (*raceyi* CMN 11430), Museum of Vertebrate Zoology (*vigilis* MVZ 418), United States National Museum of Natural History (*cascadenis* USNM 90134; *nivaria* USNM 72235; *sheldoni* USNM 137319; *oxytona* and *sibila* USNM 174503), and the British Museum of Natural History (*okanagana* BMNH 55.12.24.126).

The etymology of the specific epithet is derived from *caligatus* (L), booted, a reference to the black or blackish brown feet (Brown 1956). Common names are marmotte des rocheuses and siffleurs or siffleux (French—Banfield 1974; Howell 1915), Skwey-kwey (Ahtena or Ahtna—Richardson 1829), Thidnu (Nagailer or Carrier or Dakelh—Richardson 1829), and ground hog, whistler, whistling pig, whistling marmot, white whistler, whistler of the rocks, rockchuck, mountain marmot, watchman of the crags, and badger (English—Banfield 1974; Dufresne 1946; Howell 1915; Lechleitner 1955; Nagorsen 1990; Whitaker 1988; Woods 1980).

DIAGNOSIS

Species of the *caligata* group (*caligata*, *olympus*, *vancouverensis*) are distinguishable from other species of *Marmota* in North America by mixed black and white or solid brownish pelage, larger size (total length 630–820 mm versus 470–700 mm; Armitage 2003), circular or subcircular shape of the posterior plantar pads on the hind feet, deeper angular process of the mandible, and more well-developed sagittal and lambdoidal crests (Howell 1915). *M. caligata* differs from *M. olympus* (Olympic marmot) by having black and white pelage, black feet, smaller cranium, narrower interorbital region (24.13 mm versus 27.53 mm, males), narrower postorbital width (16.32 mm versus 16.56 mm, males), wider zygomatic width (64.24 mm versus 64.22 mm, males), anteriorly divergent upper molar toothrows and rectangular-shaped lachrymal bones (Hoffmann et al. 1979; Howell 1915). *M. caligata* differs from *M. vancouverensis* (Vancouver Island marmot) by having black and white pelage, deeply V-shaped posterior border of nasals, anteriorly divergent upper molar toothrows and rectangular-shaped lachrymal bones (Howell 1915). *M. caligata* differs from *M. broweri* (Alaska marmot) by coarse rather than soft dorsal pelage, uniformly colored or lightly tipped dorsal

guard hairs, black cap extending from nose to neck interrupted with a white patch between the eyes and nose, black lips, a longer angular process of the mandible (52.79 mm versus 47.83 mm, males), longer rostrum (27.85 mm versus 25.06 mm, males), smaller postorbital width (16.32 mm versus 16.84 mm, males), more well-developed sagittal and lambdoidal crests, gradually tapering nasals with a slightly convex or straight margin, larger mastoid width (45.12 mm versus 39.51 mm, males), and rectangular-shaped lachrymal bones (Hoffmann et al. 1979; Rausch 1953).

GENERAL CHARACTERS

Marmota caligata (Fig. 1) is a large marmot with a thick body, short and broad head, and short and stout legs (Hoffmann et al. 1979; Howell 1915). The length of the tail ranges from 30% to 51% of the length of the head and body and is densely haired and slightly flattened. The nose is broad, blunt, and covered with hair to the edge of the nostrils. The ears are small, broad, rounded, and well haired. Tufts of long, black bristles are present behind the nose, underneath and between the eye and ear, and over the eye; small, scattered bristles are present under the chin. The feet are robust; the claws are slightly curved and those on the forefeet are slightly stouter than those on the hind feet. The pollex of the forefoot is rudimentary and has a broad, flat claw; the 3rd digit is the longest, the 2nd and 4th are subequal in length, and the 5th is shorter; the plantar surface is naked, with 3 plantar pads positioned at the bases of the digits and 2 larger plantar pads positioned posteriorly. The relative lengths of the digits of the hind foot are like that of the forefoot; the plantar surface is naked except at the heel with 4 plantar pads positioned at the bases of the digits and 2 almost circular plantar pads positioned posteriorly.

The overall color is black and white (Hoffmann et al. 1979; Howell 1915), with cinnamon buff on the posterior body; dorsal coloration may also be brownish drab, russet, or Vandyke brown (Ridgway 1912). The dorsum of the head is covered with short, unicolored black hairs; a white patch extends between the eyes and across the rostrum, which is sometimes interrupted by a small black spot or band; the tip of the nose is white; the black of the cap extends posteriorly as a dark patch behind the ear or as an indistinct dark band down the neck to the shoulder. The ears are black and white. The sides of the face are grizzled black to brown, but abruptly whitish near the mouth; the lips and throat are whitish. The feet are covered with short, unicolored, black or blackish brown hairs; whitish markings often are present on the forefeet. Males and females are similar in coloration.

Pelage color varies geographically (Hoffmann et al. 1979; Howell 1915): populations of *M. c. caligata* are generally lighter colored; populations of *M. c. okanagana* are darkest in the northern part of the distribution and lightest

in the southern portion, with geographically intermediate populations being transitional in color; and populations of *M. c. cascadiensis* are darker, blackish in the north and brownish in the south. Melanistic individuals are entirely black except for some grayish hairs on the sides and neck, and small whitish patches on the venter and the nose. Pelage of *M. caligata* from Montague Island, Alaska (Dufresne 1946) and Glacier Bay, Alaska (specimens in the MVZ, USNM, and University of Alaska collections; MacDonald and Cook 2009) frequently is melanistic.

The pelage consists of 2 types of fur: long, coarse guard hairs that cover the entire body; and dense, soft, woolly underfur that covers the dorsum and sides, but is absent on the venter (Hoffmann et al. 1979; Howell 1915). Dorsal guard hairs are tricolored and bicolored. Tricolored hairs are dark basally, light in the middle, and dark at the tips. Geographic variation in pelage coloration is attributed to a wider, lighter-colored middle band and a narrower or absent dark terminal band. Light-tipped guard hairs on the neck, shoulders, and upper back give the pelage a “mantled” appearance. The cinnamon-buff coloration of the lower back and rump is due to bicolored light-tipped guard hairs, tricolored guard hairs with light middle bands, and the distal portion of the underfur becoming more buff colored. Hairs of the underfur are fine and soft, dark (gray or dark brown) basally, and lighter (gray, buff, cinnamon, or reddish brown) distally. The venter is sparsely haired, guard hairs are light colored, and most lack dark tips. Hairs of the tail are long and coarse, dark basally, light in the middle, and dark at the tips.

Ranges of external measurements (mm) for males and females, respectively (Howell 1915), were: total length, 630–785, 620–820; length of tail, 197–252, 170–247; length of hind foot, 92–112, 90–113. Ranges of cranial measurements (mm) for males and females, respectively, were: condylobasal length, 89.5–107.4, 88.7–106.5; palatal length, 51.2–62.7, 50.2–61.4; postpalatal length, 34.3–41.7, 34.0–41.1; length of nasals, 35.0–45.3, 37.0–44.0; zygomatic breadth, 61.5–69.8, 59.4–68.4; mastoid breadth, 41.3–49.2, 39.7–49.4; least interorbital breadth, 22.5–29.0, 21.9–27.2; breadth of rostrum, 20.5–25.2, 19.3–25.0; length of maxillary tooththrow, 21.8–24.1, 21.0–24.4.

Body mass is lowest at emergence from hibernation and highest at the onset of hibernation (Barash 1989; Hock and Cottini 1966). In years of late snowmelt and short foraging season, the body mass of females entering hibernation (\bar{X} = 3.9 kg) is not significantly different than mass at emergence (\bar{X} = 3.3 kg); during normal years, prehibernation mass (\bar{X} = 4.9 kg) is significantly greater than that at emergence (\bar{X} = 3.6 kg—Holmes 1984a). Approximate seasonal mass (kg) of 4 age groups (Barash 1989; estimated from figure 1.8) is: adults, 3.75 (May), 7.0 (September); 2-year-olds, 2.75 (May), 6.0 (September); yearlings, 1.5 (June), 4.25 (September); young, 1.25 (July), 2.5 (September). Average rate of mass increase for yearlings is 31.4 g/day in July and 27.8 g/day in August (Barash 1989).

Marmota caligata exhibits sexual, age, and geographic variation. Males and females are sexually dimorphic in body size and cranial dimensions, with males being significantly larger, except in *M. c. cascadiensis* (Hoffmann et al. 1979). Young, yearlings, and adults may be differentiated by size (Barash 1974, 1989); for both sexes, breadth of the zygomatic arch discriminates age classes (juveniles, yearlings, 2-year-olds, 3-year-olds, and ≥ 4 -year-olds) in ecological studies (Karels et al. 2004a). Geographic variation in head and body size is present, but is not clinal; individuals are smaller in the north (Alaska, including island populations, northern Yukon, and British Columbia), larger in the central portion of the distribution, and smaller in the southern part of the distribution (southern British Columbia, Alberta, Montana, and Idaho); populations of coastal Washington and British Columbia are larger in size (Hoffmann et al. 1979).

The skull (Fig. 2) is short and broad, with a nearly straight superior outline (Hall 1981; Howell 1915). The postorbital constriction is broad and the interorbital region is narrow; the postorbital processes generally project posteriorly rather than at right angles to the long axis of the skull. The rostrum is short and broad. The nasals are long, extending to or just beyond the ends of the premaxillae; the nasals narrow posteriorly, the width at the posterior ends being about the same width as the premaxillae. The zygomata are broadly expanded posteriorly. Temporal ridges are present and in older individuals unite to form a pronounced sagittal crest. The anterior portion of the floor of the basioccipital is nearly flat and bordered posteriorly by 2 processes that unite at about the midportion and continue to the foramen magnum as a pronounced ridge. Two pronounced depressions on either side of the median ridge often are present on the anterior portion of the basioccipital. The posterior border of the palate is beveled, the interpterygoid fossa is relatively narrow, and the palatal foramina are variable in shape. Molar teeth are similar to those of *M. monax* (woodchuck), maxillary toothrows are convergent posteriorly, and the anterior faces of the incisors are ivory yellow to orange buff in color.

The dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22. Dental characters include: P4 is as large as or larger than M1; cheek teeth are high crowned; metalophs of M1–M3 are complete; metaloph of M3 is oriented posteriad and joins the posterior cingulum; p4 is molariform and the protolepid is a transverse crest between parametaconid and protoconid; and in occlusal outline, m1 and m2 are shaped like parallelograms (Hall 1981).

DISTRIBUTION

Marmota caligata occurs in central Alaska, Yukon Territory, and western Northwest Territory, central and northern British Columbia, the Cascade Mountains of Washington and southern British Columbia, the Bitterroot



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Marmota caligata* (OMNH [Sam Noble Oklahoma Museum of Natural History] 2183) from Upper Cabin, Dry Creek, Alaska. Greatest length of skull is 95.80 mm. Photograph by MAM.

Mountains of Idaho, and the Rocky Mountains of Alberta and western Montana (Fig. 3; Barash 1980; Cowan and Guiguet 1978; Hall 1981; Howell 1915; Thorington and Hoffmann 2005; Youngman 1975). The distribution in major regions of Alaska is given by MacDonald and Cook (2009) and was further clarified by Gunderson et al. (2009).

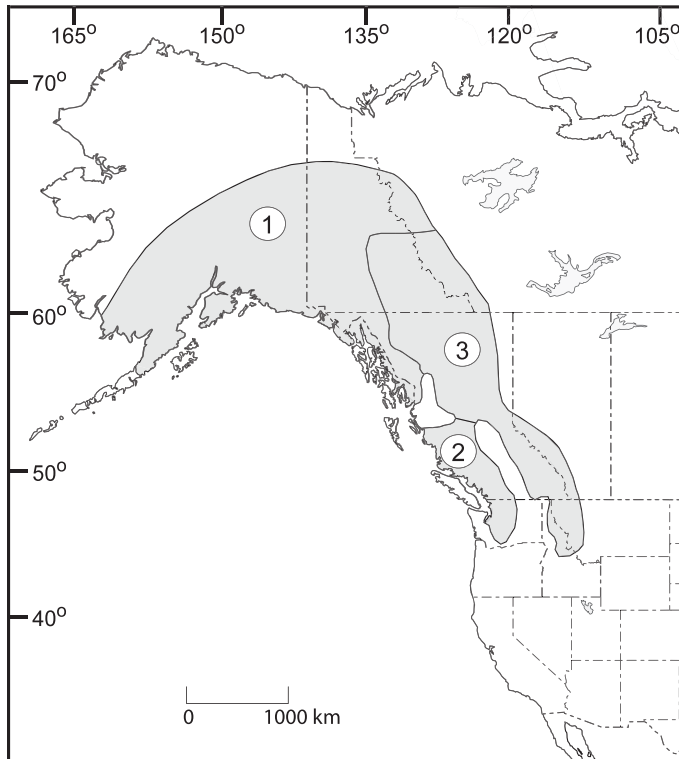


Fig. 3.—Geographic distribution of *Marmota caligata*. Map redrawn from Hall (1981) with modifications on the basis of Hoffmann et al. (1979) and MacDonald and Cook (2009): 1, *M. c. caligata*; 2, *M. c. cascadiensis*; 3, *M. c. okanagana*.

Although *M. caligata* is found north of the Yukon River in the Ogilvie Mountains in Yukon Territory, in Alaska, the Yukon River forms the boundary between the distributions of *M. caligata* and the Alaska marmot (Gunderson et al. 2009). Elevation ranges from near sea level in northern Alaska to about 1,900 m in Yukon Territory and 1,200 m in south-central Alaska, and from 1,600 to 2,500 m in the Coastal Mountains, Rocky Mountains, and Cascade Range (Banfield 1974; Barash 1974, 1980, 1989; Dixon 1938; Gray 1967; Hock and Cottini 1966; Holmes 1984a, 1984b; Knapp 1977; Kyle et al. 2007; Noyes and Holmes 1979; Taulman 1975, 1977, 1989, 1990a, 1990b; Tyser and Moermond 1983).

FOSSIL RECORD

Fossils of *Marmota* are known from the early Pleistocene of western Alaska (Cape Deceit Local Fauna; Guthrie and Matthews 1971). Remains of *M. caligata* have been found at Pleistocene and Holocene localities in central Alaska (Broken Mammoth site) and western Alaska (Trail Creek caves—Yesner 2001; as *M. flavescens*) and in 2 caves on Prince of Wales Island—an island not currently inhabited by *M. caligata*. An incisor from Devil's Canopy Cave had a radiocarbon date $\geq 44,500$ years ago (Heaton 1995a; Heaton and Grady 2003; Heaton et al. 1996) and a $\delta^{13}\text{C}$

value of -23.7% , indicating a diet of terrestrial plants (Heaton 1995b). Remains from On Your Knees Cave had radiocarbon dates ranging from 39,900 to $23,560 \pm 770$ years ago (Heaton and Grady 2003). Marks and placement of bones in On Your Knees Cave suggest that foxes used the site for scavenging or predation (Hansen 2005). Populations of *M. caligata* on Prince of Wales Island may have been affected negatively during the Last Glacial Maximum because fossils predate the late-Wisconsin glacial maximum (21,000–16,000 years ago; Blaise et al. 1990). No remains are known from postglacial deposits and the island was not successfully recolonized (Heaton 1995a; Heaton and Grady 2003; Heaton et al. 1996). Remains are known from postglacial deposits in central Alaska (Georgina 2001: Lime Hills Cave I; 8,385–10,360 years ago; Yesner 2001). A specimen is known from an archaeological site on Kodiak Island (USNM 256721; MacDonald and Cook 2009), although *M. caligata* is not currently found on the islands of southwestern Alaska.

FORM AND FUNCTION

Form.—*Marmota caligata* has 5 pairs of mammae (2 pectoral, 2 abdominal, 1 inguinal), although individuals with 4 pairs and 4 pairs plus 1 unpaired teat have been reported (Hoffmann et al. 1979; Howell 1915; Moore 1961).

In *Marmota*, the morphology of the mandible and ventral cranium do not exhibit size- and shape-related convergence. Convergent morphology due to ecological similarities is insignificant (Cardini 2003; Cardini and O'Higgins 2005). *M. caligata* exhibits sexual dimorphism in allometry and in shape. Shape variation is significantly correlated with size, with 43.6% (mandible) and 37.6% (ventral cranium) of shape change explained by ontogenetic scaling. Areas of the mandible and ventral cranium related to mastication exhibit the greatest modifications. Malocclusion due to unrestricted incisor growth is known to occur. In 1 specimen, the upper incisors curved to the left for about 1.5 revolutions, with a length of 11.5 cm and the lower incisors curved to the right with a maximum length of 6.5 cm (Elliott 1989); the upper right incisor of a specimen curled 1.5 times, with a diameter of 33.5 mm (Pratt and Knight 1981). *M. caligata* has 21 caudal vertebrae (Hoffmann et al. 1979).

The anatomy of the digestive, respiratory, circulatory, and urogenital systems of *M. caligata cascadiensis* generally is similar to that of *Cynomys* and other species of squirrels (Wright 1962). The outer surface and lining of the esophagus has pleated longitudinal folds that vary in shape and size. A short constriction anterior to the pyloric valve may be present and the walls of the stomach are firm or flexible, depending on the extent of distribution of the outer longitudinal muscle and transverse fibers and thickness and surface texture of the lining. The duodenum, jejunum, and ileum of the small intestine generally are undifferentiated.

ated. The cecum is large and undivided; the lining has deep, transverse rugae with smaller rugae forming cross-ridges. The ileocecal valve is positioned dorsally, slightly inferior, and sinistral to the cecocolic junction. A vermiform process is absent. The ascending colon is formed by 2 long, reflexed, fingerlike projections connected by a vascularized, fatty mesentery.

The morphology of the accessory digestive organs was described by Wright (1962). The omentum is located between the stomach and the intestines rather than in front of the intestines as in many mammal species. The anterior portion of the greater omentum attaches to the duodenum and stomach and the posterior portion attaches to the pancreas and transverse colon. The lesser omentum lacks fat deposits and connects the stomach to the liver. The pancreas generally is comprised of 2 lobes. The liver consists of 4 lobes, although the right lateral and caudate lobes may be joined. A small (0.2 cm), narrow projection present on the papillary lobule of the liver of individuals captured in late summer may correspond to the accessory or hibernal lobe that develops in some mammal species before hibernation as a reserve nutrient supply that disappears at the termination of hibernation. The gall bladder is an elongated sphere positioned in a notched depression of the cystic lobe of the liver. Ranges of measurements for digestive organs (cm, $n = 4$ except as noted; presented as either length or length by width where appropriate) were: length of the digestive tract from esophagus to anus, excluding the stomach and cecum, 404.8–582.4; length of esophagus, 17.0–20.8; length of small intestine, 251.2–380.0; length of large intestine, 130.0–183.0; stomach, 11.0–20.0 by 6.5–12.0; cecum, 14.3–25.0 by 4.0–5.8; length of 1st colic loop, 27.0–37.6; length of 2nd colic loop, 31.4–63.0; omentum ($n = 3$), 18.0–28.0 by 29.0–35.0; cystic lobe of liver, 6.0–7.7 by 10.0–13.3; left lateral lobe of liver ($n = 3$), 7.5–8.3 by 9.3–17.2; right lateral lobe of liver, 4.0–5.7 by 5.0–7.2; caudate lobe of liver, 4.5–7.5 by 3.5–4.3; gall bladder, 2.8–5.0 by 2.0–3.8; length of cystic duct, 2.8–5.0; length of dorsal portion of pancreas ($n = 3$), 11.0–17.0; and length of anterior portion of pancreas ($n = 3$), 21.0–29.5.

The morphology of the respiratory system was described by Wright (1962). The thyroid, arytenoid, and cricoid cartilages form the anterior, posterior, and basal components of the larynx, respectively. Two folds of tissue cover the triangular-shaped glottis and a small slit is present in a small circular fold of tissue at the base of the epiglottis. The number of C-shaped cartilaginous rings of the trachea varies among individuals. The right lung generally consists of 4 lobes; in some individuals the superior and inferior lobes are partially joined and the notch in the postcaval or median lobe varies from small to deep. The left lung is a single lobe as in *Cynomys*, but unlike some other sciurids (e.g., *Sciurus griseus*—western gray squirrel, *Spermophilus richardsoni*—Richardson's ground squirrel) in which 2 lobes are present. The morphology of the heart, vessels, and spleen are

uniform among individuals and similar to that described for other mammal species. Ranges of measurements associated with the respiratory system (cm, $n = 4$; presented as either length or length by width where appropriate) were: larynx, 2.0–2.5 by 1.5–2.3; length of trachea, 8.0–10.0; superior lobe of right lung, 4.0–6.2 by 4.0–8.5; middle lobe of right lung, 2.7–5.0 by 5.0–8.7; inferior lobe of right lung, 6.2–8.9 by 5.6–7.5; postcaval lobe of right lung, 3.5–5.5 by 6.4–7.5; and left lung, 8.5–12.4 by 4.0–6.0.

The urinary system is similar to that described for *Cynomys* (Wright 1962). Unlike males, the female system is not enclosed in fatty mesentery, and the urethra is shorter and not connected to the genital tract. In males, coagulating and vesicular glands are absent, and the Cowper's gland and bulbar gland are small. The prostate gland is a large, lobed, irregular mass surrounding the posterior and lateral portions of the urethra. The glans penis is simple and small; the baculum is asymmetrical. In females, the uterus is duplex and the cervix is divided internally by a structure measuring 1.7 cm. Ranges of measurements associated with the urinary system (cm, $n = 4$ except as noted) were: length of right kidney, 2.4–6.3; width of right kidney, 3.6–4.0; length of right ureter, 13.7–15.0; length of bladder ($n = 3$), 2.8–4.7; width of bladder ($n = 3$), 3.0–5.0; length of right testis ($n = 3$), 3.6–3.8; width of right testis ($n = 3$), 1.6–2.2; length of right ductus deferens ($n = 2$), 9.5–11.0; length of right ovary ($n = 1$), 0.4; width of right ovary ($n = 1$), 0.2; length of uterus including the cervix ($n = 1$), 9.5; width of uterus including the cervix ($n = 1$), 0.5; length of vagina ($n = 1$), 4.0; and width of vagina ($n = 1$), 0.7.

Sudoriferous exocrine cutaneous facial glands (face and perioral glands) are located in the dermis and consist of aggregations of coiled or branching tubular structures (lobules) with ducts that open to the cutaneous surface (Rausch and Bridgens 1989). Gland secretions are yellowish and aromatic. Face and perioral glands show age and seasonal variation in morphology, but sexual variation is absent. Glands are fully developed in individuals at least 3 years of age and are largest in breeding males. Gland development and secretory activity is correlated with the reproductive cycle—greatest in the spring and declining during summer and autumn. Face glands are located in a triangular area between the ear and eye. The number of lobules per gland ranges from 10 to 30 and the greatest diagonal dimension ranges from 30 to 40 mm. Openings of the ducts of the lobules are indicated by small black spots ranging from 140 to 225 μm in diameter. A pigmented ring, ranging from 262 to 375 μm in diameter, surrounds each opening, which is adjacent to or encloses a guard hair. During maximal development, face glands appear as prominent bulges; lobules are ellipsoidal to rectangular in shape and have a vertical diameter of about 7 mm. In young individuals and when inactive, lobules are small and flattened and measure 1.5 to 4.5 mm. Perioral glands are positioned in the lower lips,

opposite the diastema between the mandibular cheek teeth and the lower incisors. Glands are round to ovoid in shape, with a diameter ranging from 8 to 12 mm. Although similar to face glands, the lobules are more closely apposed and the ducts of each gland open separately at the surface at the mucocutaneous junction just anterior to the angulus oris. Anal glands are positioned at the mucocutaneous junction deep to the anal sphincter, and superficial to the underlying voluntary muscle. In response to stress, 3 papillae are protruded from the anus. Anal gland secretions are stronger and more aromatic than secretions of the glands of the head.

Function.—*Marmota caligata* has 1 molt/year that begins in early to mid-summer (Hoffmann et al. 1979; Howell 1915). New pelage appears randomly over the body, although the pelage on the rump, base of tail, and tail may be replaced every 2nd or 3rd year. Young have 3 juvenile pelages (Hoffmann et al. 1979). The 1st pelage is dense, soft, and woolly. In the 2nd pelage, guard hairs of the 1st pelage are shed. In the 3rd pelage, the 2nd set of hairs grows through the 1st set, resulting in the adult color and pattern.

Body mass increases and fat accumulates under the skin and in the body cavities after the breeding season (Bailey 1918). Approximately 47% of body mass is lost during hibernation (13.8 g/day over 7.5 months—Armitage and Blumstein 2002) and varies by age group (Barash 1989; estimated from figure 1.9): young to yearling, 25%; yearling to 2-year-old, 37%; and 2-year-old to adult, 43%. Total mass loss during hibernation is correlated with immergence mass, suggesting the relation to maintenance during hibernation and postemergence environmental stress (e.g., periods of heavy snow when forage is not available); however, body mass and mass loss are not correlated with length of hibernation (Armitage and Blumstein 2002; Barash 1989). Social thermoregulation was predicted to occur in *M. caligata* on the basis of social system and group hibernation (Armitage and Blumstein 2002). The social structure of *M. caligata* in the Yukon Territory, however, was found to have only a minor influence on survival or reproduction (Patil 2010).

Large body mass and absolute gut capacity may compensate for a simple digestive tract (Hume et al. 1993). *M. caligata* digested 57.6%, 50.3%, and 81.0% of total dry matter on fiber diets of 22%, 28%, and 7%, respectively. Transit time was 13.1 h for fluid and fine particles and 17.1 h for large particles. Mean retention time was 24.8 h for fluid and fine particles and 28.9 h for large particles, indicating no selective retention of fluid digesta. Hiccups are known to occur in young and other age classes (Taulman 1975).

ONTOGENY AND REPRODUCTION

Reproductive maturity of *Marmota caligata* is reached at 3 years of age and relative reproductive effort is low (0.30—Barash 1989); delay of sexual maturation is correlated with altitude (Wasser and Barash 1983). Females breed

biennially (in alternate years—Barash 1974, 1980, 1989; Wasser and Barash 1983), although breeding in successive years has been reported (Kyle et al. 2007). Females may skip a reproductive year and not breed for 2 consecutive seasons. Reproductive skipping is not correlated with age or habitat quality; is more frequent among bigamously mated females that are reproducing synchronously with a cofemale; and is more frequent among subordinate than among dominant females (Wasser and Barash 1983). Litters are spaced 2 to 4 years apart with a mean of 3.3 years (Holmes 1984a).

The anatomy and physiology of the testes and ovaries is similar to that described for the woodchuck by Rasmussen (1918; Rausch and Bridgens 1989). Testes exhibit little reproductive activity in early spring; testes return to an intra-abdominal position followed by a decrease in size of interstitial cells and testes (Rausch and Bridgens 1989). Testes are enlarged and descended only in males at least 3 years of age (Barash 1989). During late May, females have swollen vaginas and exhibit characteristic estrus behavior that is absent by mid-June (Barash 1981). Breeding occurs in mid- to late May during the 1st few weeks after emergence from hibernation (Armitage and Blumstein 2002; Barash 1974, 1980, 1981; Holmes 1984a); breeding has been suggested to occur in dens before emergence in the spring (Hock and Cottini 1966; Kyle et al. 2007) or in autumn (Hock and Cottini 1966), although the latter is considered unlikely.

The reproductive cycle (copulation to weaning) is about 10 weeks (Barash 1989). Gestation ranges from 25 to 30 days (Barash 1980, 1981; Holmes 1984a). Birth occurs underground in early May (Dixon 1938) or early to mid-June (Bailey 1918; Barash 1980). Females with 2 (Hock and Cottini 1966), 5 (Bailey 1918; Howell 1915), and 6 (Rausch and Bridgens 1989) embryos have been reported. Litter size averages 3.9 (Barash 1989), ranges from 2 to 5 (Barash 1975a, 1980; Gray 1967; Holmes 1979; Taulman 1975; Taylor and Shaw 1927), and is largest early in the season and smallest late in the season (Barash 1989). Older females have larger average litter sizes than females breeding for the 1st time, 4.2 and 2.3, respectively; however, litter size does not increase with age after the initial breeding effort (Barash 1989). Dominant females have a higher reproductive success than subordinate females (means; Wasser and Barash 1983): number of young, 4.3 versus 2.2; number of yearlings, 2.7 versus 0.5; number of nondispersing 2-year-olds, 0.9 versus 0.2. Young 1st appear aboveground from early June to early August (Barash 1974; Dixon 1938; Gray 1967; Holmes 1984a; Karels et al. 2004b; Patil 2010; Taulman 1975, 1977, 1990b) when about 3–4 weeks of age; at this time the pelage is well developed, eyes are open, and the young are ambulatory (Barash 1980, 1981). Young of dominant females emerge earlier than those of subordinate females (Barash 1989). The lactation ranges from 25 to 30 days (Blumstein and Armitage 1998; Holmes 1984a); young are

weaned between the 3rd week of July and 1st week of August (Barash 1989) and weaning is advanced or complete (Barash 1980) when young appear aboveground.

ECOLOGY

Population characteristics.—*Marmota caligata* is colonial; colonies cover from 1.1 to 12 ha (Barash 1973; Taulman 1977, 1990a, 1990b; Tyser 1980) and densities range from 0.6 to 7.8 animals/ha (Barash 1989; Taulman 1975); mean home range is 13.8 ha (Holmes 1979) and mean foraging area is 9.2 ha (8.9–10.0 ha; Holmes 1984b). Colony sizes range from 2 to 36 (Barash 1973, 1975a, 1989; Gray 1967; Karels et al. 2004b; Kyle et al. 2007; Taulman 1975, 1977, 1990a) and generally consist of 1 adult male (occasionally a 2nd “satellite” male), 1–3 adult females, 0–5 2-year-olds, 0–6 yearlings, and 1–5 young of the year (Barash 1974, 1975a, 1980, 1989; Gray 1967; Holmes 1979, 1984a; Noyes and Holmes 1979; Taulman 1975, 1977, 1990a). “Satellite” males generally are present in larger or polygynous colonies and are subordinate to, and younger than, the adult male (Barash 1989). Colonies generally are isolated, but when contiguous may form a “colony town” (Barash 1989). Members of a colony do not maintain territories and do not defend foraging areas within the colony (Barash 1974; Holmes 1984b). Population abundance in southwest Yukon Territory varied, from 66 in 1999, a peak of 146 in 2002, and declined to 80 in 2004; variation in population growth rates was determined largely by juvenile and adult survival (Patil 2010).

Percentage of young that survive the 1st winter is 71% (Holmes 1984a; Taulman 1975) and is highest (about 70% estimated from Barash 1989; figure 11.1) for young that were weaned during the middle of the season (last week of July) and lowest for young weaned during the 1st week of August (about 25% estimated from Barash 1989; figure 11.1). Juvenile survival in Yukon Territory varied from 40% to 95% over 5 years and was primarily influenced by winter climate and secondarily by social group size (Patil 2010). Survivorship of male and female young of the year (56% and 54%, respectively) and male and female yearlings (88% and 83%, respectively) is not biased as to sex; survivorship of 2-year-olds is biased toward females (61% and 85%, males and females, respectively—Barash 1989). Breeding females have greater winter mortality (68%) than nonbreeding females (Barash 1989). Survival of *M. caligata*, especially juveniles, in Yukon Territory is correlated with intensity of the winter as measured by the mean winter Pacific Decadal Oscillation (PDO) index (Patil 2010). Winters with high PDO values, corresponding to shallow snowpack and early spring snowmelt, had a negative impact on *M. caligata* survival (Patil 2010). When snow cover is heavy, mortality is low among all age groups; when snow cover is low, mortality is high for hibernating young of the year (Barash 1989). Life

span is at least 9 years, as individuals of 7 and 9 years of age are known to reproduce (Barash 1989; Kyle et al. 2007). The breeding ratio is 1.1:1 (male : female) and is related to mean distance to nearest-neighbor hibernaculum (negatively) and vegetation biomass (positively). Ratios were 1:1.7 and 1:1 at interburrow distances of 145 m and 259 m, respectively, but were 1:1 and 1:2 when vegetation biomass was < 150 g/m² and 325 g/m², respectively (Holmes 1984a).

Marmota caligata disperses or moves to the periphery of their natal colony when 2 years of age (43% dispersed), although 3-year-olds (Barash 1989; Blumstein and Armitage 1997; Holmes 1984a) or older individuals (5-year-olds) also may disperse (Kyle et al. 2007). Dispersal is correlated with the presence of new litters in a colony (86% of dispersers resided in colonies with new litters), is sex biased (68% males and 25% females), and is related to winter mortality (2-year-olds are less likely to disperse if mortality is high). Transients may comprise about 2% of a resident population (Barash 1989).

Space use.—*Marmota caligata* occurs at or above timberline on alpine and subalpine rockslides, boulder piles, or talus slopes surrounded by meadows in western North America (Anderson 1934; Barash 1974, 1989; Dixon 1938; Gray 1967; Karels et al. 2004b; Tyser 1980; Tyser and Moermond 1983). Plant communities include herbs, grasses, sedges, and often krumholtz (elfin forest) islands (Barash 1974, 1989; Tyser 1980; Tyser and Moermond 1983) and common plant species are: yellow avalanche-lily (*Erythronium grandiflorum*), alpine arnica (*Arnica alpina*), mountain sorrel (*Oxyria digyna*), Lyall's lupine (*Lupinus lyalli*), old man's whiskers (*Geum triflorum* var. *campanulatum*), marigolds (*Caltha leptocarpa*), Hudson's anemone (*Anemone multifida* var. *hudsoniana*), pioneer violet (*Viola glabella*), eightpetal mountain-avens (*Dryas octopetala*), netleaf willow (*Salix reticulata*), sedges (*Carex*), and subalpine fir (*Abies lasiocarpa*—Barash 1974, 1989; Patil 2010; Tyser 1980; Tyser and Moermond 1983).

Seasonal movement occurs in some colonies of *M. caligata*. Colonies may move from higher elevations to lower elevations in autumn (Hock and Cottini 1966) or, after emergence, move to areas as the snowpack melts (Barash 1974, 1989).

Colonies maintain separate burrows for hibernation, sleeping, and escape from predators (refuge). Burrows (88%) are located between boulders in talus (Barash 1973, 1989; Karels et al. 2004b; Taulman 1975). Number of burrow openings/ha range from 5.9 (Taulman 1975) to 32, 45, and 49 (Barash 1989); trails connect frequently used burrows (Barash 1989; Dixon 1938; Gray 1967). A colony generally uses a single burrow for hibernation (Barash 1989; Holmes 1984a), although 2 burrow systems may be used (33% of cases—Barash 1989). The hibernaculum often is the largest and oldest burrow and may be used as the primary burrow during the summer; plugging of hibernacula has not been reported (Barash 1989). The number of sleeping burrows ranges from 4 to 9 (Gray 1967; Taulman 1975, 1990a,

1990b); sleeping burrows have multiple (3–5) entrances and measure 3.5 m in length (Holmes 1984b). Mounds of gravel, rocks, and debris are present at the entrances of hibernation and sleeping burrows and extend downhill in an arc (Gray 1967; Taulman 1975). Refuge burrows generally are located in meadows (Holmes 1984a, 1984b) and number 25 (British Columbia—Gray 1967), 68 (Washington—Taulman 1975, 1990a, 1990b), and 65–120 per colony (south central Alaska—Holmes 1984b); an average of 5.5 new burrows is dug each year (Holmes 1984a). Refuge burrows have a single entrance and measure 1–2 m in length (Holmes 1984a, 1984b). Existing burrows are enlarged by using the forelegs to scoop dirt and rocks beneath the body and tail and using the hind legs to kick it out of the opening; dirt is pushed out of the burrow and down the slope of the mound using the forelegs; rocks are carried to the surface using teeth (Gray 1967; Taulman 1975). Grass, gathered in early summer (dried plant material) and late summer (living plant material), is carried into burrows and likely used in nest construction (Bailey 1918; Barash 1989; Dixon 1938; Gray 1967; Taulman 1975). Material from the previous year is discarded after emergence from hibernation (Dixon 1938).

Burrows (occupied and unoccupied) are used by all members of a colony (Barash 1974, 1989). Although 1 sleeping burrow generally is preferred (Barash 1974, 1989), sleeping burrow fidelity decreases from June to August (Barash 1989; Taulman 1975), and in September individuals begin using the same burrow for sleeping (Taulman 1975, 1990b). Burrow fidelity is highest for parous females and their young, and lowest for adult males; older individuals and males are less likely to share sleeping burrows (Barash 1989).

Diet.—*Marmota caligata* is a diurnal herbivore and shows a seasonal preference for plant species and parts; leaves of herbaceous plants are eaten in early summer, flowers of herbaceous plants in midsummer, and herbs and forbs in late summer (Barash 1989; Taulman 1975, 1990b). Selection is unrelated to availability or aboveground biomass (Hansen 1975) or nutrient content (Holmes 1984b). In south-central Alaska, > 90% of the diet consisted of alpine arnica (*Arnica alpina*), rough fescue (*Festuca altaica*), Sitka valerian (*Valeriana sitchensis*), Ross' avens (*Geum rossii*), fireweed (*Chamerion angustifolium*), and meadow buttercup (*Ranunculus acris*), with sedges (*Carex*) comprising 78.0–91.2% of the total dry weight (Holmes 1984b). On the Kenai Peninsula, Alaska, 28 species are eaten, although 90% of the diet is comprised of locoweed and milkvetch (*Oxytropis* and *Astragalus*), sedges (*Carex*), fleabanes (*Erigeron*), fescues (*Festuca*), mosses, lichens (*Cladonia*), mountain-avens (*Dryas*), and willows (*Salix*—Hansen 1975). In British Columbia, white pasqueflower (*Pulsatilla occidentalis*), Indian paintbrush (*Castilleja*), yellow avalanche-lily (*Erythronium grandiflorum*), lupine (*Lupinus*), bracted lousewort (*Pedicularis bracteosa*), ragwort (*Senecio*), grouseberry (*Vaccinium scoparium*), and false

green hellebore (*Veratrum viride*) were most commonly eaten (Gray 1967). Bark (Lechleitner 1955), cardboard (Gray 1967), and horse oats (Bailey 1918) also are eaten. Carnivorous and cannibalistic behavior is known; hair and bones of adult marmots have been found in scats, possibly a result of scavenging (Barash 1989). Water is obtained from standing water, moisture from plants, and dew (Barash 1989); snow also is eaten (Barash 1989; Gray 1967). Salt is obtained from rocks and soil, but *M. caligata* is attracted to higher concentrations present at human urine sites (Taulman 1975, 1989; see also Holmes 1979, 1984a).

Diseases and parasites.—Ectoparasites include the fleas (Siphonaptera: Ceratophyllidae) *Thrassis pristinus*, a host-specific flea (Holland 1963; Rausch and Rausch 1971), and *Dasyptyllus stejnegeri*, a rare parasite of land birds (Rausch and Rausch 1971). Endoparasites include the cestodes (Cestoda: Anoplocephalidae) *Catenotaenia reggiae* and *Diandrya composita*, which were found in 72% of *Marmota caligata* examined. Infection by cestodes occurs when the intermediate host (mites) is ingested during feeding (Rausch and Rausch 1971). Individuals collected in the spring have lower rates of infection due to the loss of cestodes during hibernation (Rausch and Rausch 1971). *M. caligata* is an intermediate host for the cystic larval form of the cestode *Taenia mustelae* (Rausch 1977 not seen, cited in Samuel and Pybus 2001).

Interspecific interactions.—Predators of *Marmota caligata* include golden eagle (*Aquila chrysaetos*), kestrel (*Falco sparverius*), lynx (*Lynx canadensis*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), grizzly or brown bear (*Ursus arctos*), black bear (*Ursus americanus*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), and cougar (*Puma concolor*—Bailey 1918; Barash 1975b, 1989; Dixon 1938; Dufresne 1946; Holmes 1979, 1984b; Lechleitner 1955; Noyes and Holmes 1979; Olendorff 1976; Patil 2010; Rausch and Rausch 1971; Taulman 1975, 1990a, 1990b). In Mount McKinley, Alaska, *M. caligata* was found in 8% of wolf scats and 6% of golden eagle pellets, but was a minor food item for red fox and grizzly or brown bear; percent abundance in wolf scats increased (37%) with decreasing populations of reindeer (*Rangifer tarandus*—Murie 1944). Grizzly bears will attempt to dig *M. caligata* out of dens (Bailey 1918; Barash 1989).

Marmota caligata is found in association with the woodchuck and yellow-bellied marmot (*M. flaviventris*). In the Bitterroot and Anaconda-Pintler Mountains of Montana, *M. caligata* is sympatric with the yellow-bellied marmot; *M. caligata* inhabits the alpine habitats at high elevations and the yellow-bellied marmot is found at lower elevations although it occurs in alpine habitat where *M. caligata* is absent (Hoffmann 1974). In east-central Alaska where it is sympatric with the woodchuck, *M. caligata* is restricted to talus and the woodchuck is found in predominantly loess soils along the arid lowland river valleys (Rausch and Rausch 1971). In Alaska and Yukon Territory, *M. caligata* occurs with the collared pika (*Ochotona*

collaris) and Arctic ground squirrel (*Spermophilus parryi*)—Broadbrooks 1965; MacDonald and Jones 1987; Patil 2010) where the former gathers and stores *M. caligata* fecal pellets for consumption (Taylor and Shaw 1927). In Montana, *M. caligata* occurs with the American pika (*Ochotona princeps*) and Columbian ground squirrel (*Spermophilus columbianus*)—Barash 1973, 1989; Tyser 1980; Tyser and Moermond 1983). In areas where *M. caligata* occurs with pikas and ground squirrels, such as Yukon Territory and Montana, the species separate ecologically. *M. caligata* forages at an intermediate distance from the talus (pikas forage primarily on the talus and ground squirrels in areas of new plant growth), hibernates (pikas hoard food), and like ground squirrels, concentrates foraging during June and July (pikas foraged intensely in August—Barash 1973, 1989; Patil 2010; Tyser 1980; Tyser and Moermond 1983). In Yukon Territory, *M. caligata* occurs with other mammalian herbivores, including the Arctic ground squirrel, long-tailed vole (*Microtus longicaudus*), singing vole (*M. miurus*), root vole (*M. oeconomus*), and northern red-backed vole (*Myodes rutilus*)—Patil 2010). In the Cascade Range of Washington, *Marmota caligata* occurs with the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*), yellow-pine chipmunk (*Tamias amoenus*), North American deer mouse (*Peromyscus maniculatus*), creeping vole (*Microtus oregoni*), and northern pocket gopher (*Thomomys talpoides*)—Taulman 1975). In North Cascade Mountains of Washington, a porcupine (*Erethizon dorsatum*) quill (2.91 cm) was found embedded in the ulna of a *M. caligata*, although it is not clear if the quill was injected during an encounter or encountered accidentally (Martin and Rozdilsky 1980).

Miscellaneous.—Individuals can be distinguished on the basis of pelage features (Barash 1974, 1989; Holmes 1984a, 1984b), although differentiation may be unreliable at distances over 50 m (Taulman 1975). *Marmota caligata* can be live-captured using traps baited with urine and live vegetation (Karels et al. 2004b; Patil 2010), peanut butter (Taulman 1975), and peanut butter and apples (Barash 1974); however, Holmes (1979, 1984a) found that only human urine attracted marmots into traps (Holmes 1979, 1984a). Individuals are captured as they emerge from hibernation by placing a live trap in the snow tunnel leading to a hibernation burrow (Holmes 1979, 1984a). Young are not trappable (Taulman 1975), but individuals within 2 weeks of emergence may be noosed with a nylon-coated stainless steel braided wire (60-pound test fishing line) fixed to the end of a 4-m telescopic fiberglass pole (Karels et al. 2004b). Marking methods include ear tags, dye, fur clipping, and colored wire or colored construction flagging (Holmes 1979, 1984a, 1984b; Karels et al. 2004b; Patil 2010; Taulman 1975). Counts of fecal pellets provide estimates of group size for long-term monitoring of populations (Karels et al. 2004b). *M. caligata* can be maintained in captivity at about 20°C under a 14L:10D cycle on a diet of rodent and rabbit chows (Hume et al. 1993).

BEHAVIOR

Grouping behavior.—*Marmota caligata* is highly social, with the 2nd highest social complexity index (1.35) of any sciurid (Blumstein and Armitage 1997, 1998) and exhibits monogamy or polygyny (Barash 1974, 1989; Holmes 1979, 1984a; Wasser and Barash 1983). Monogamous and polygynous colonies are found throughout the range of *M. caligata* and the social system of a colony may change between years (Barash 1989; Kyle et al. 2007). Mating system may reflect resource availability, habitat quality, or male fitness at the local level (Holmes 1979, 1984a; Kyle et al. 2007), but is not related to the harshness of the environment (Kyle et al. 2007).

During the 2-week breeding period, a mated pair will stay in proximity and show more frequent nose-body contact, following, and body touching (Holmes 1984a). Considered mate guarding (Barash 1981), the behavior is exhibited by males early in the season when females are fertile and initiated by males rather than females (Barash 1981). Males that gallivant (seek to gain extra copulations) are polygynous and have females that are nonreproductive (Barash 1981).

Play or “wrestling” is the most common social interaction and occurs most frequently among young (38%), yearling (53%), and 2-year-olds (Barash 1974; Gray 1967; Taulman 1975), especially during June and July (Gray 1967). Play bouts begin with both individuals performing “nose-up” postures, followed by about 10 s of sparring or batting with front paws, nipping or biting, and tug-of-war with locked teeth; pauses between bouts are used for repositioning, chasing, looking around, touching, or grooming (Gray 1967; Taulman 1975). Upright play-fights also occur between individuals and, among adults, 39% escalate to fights followed by chasing and pursuit (Barash 1974).

Greeting activity is correlated with activity periods and behaviors including sniffing of a distant individual, nose-to-nose contact, mouth-to-mouth contact with or without tooth locking, face chewing, and chewing of the neck and back (Barash 1974; Gray 1967). Social tolerance among colony members is high (Barash 1974), but social interactions increase before hibernation (Taulman 1990b). Grouping behavior is absent and individuals forage separately during most of the season, except when the colony is small (Barash 1974; Gray 1967; Taulman 1975, 1990b); by mid-September group foraging (due to the reduction of vegetation) is common (Taulman 1975, 1990b). Also by mid-September, boulder sharing during resting periods and social grooming is common (Taulman 1990b).

Most social interactions are intracolony (> 95%) and intrusions into adjacent or other colonies are infrequent (Holmes 1984a, 1984b). Agonistic encounters (chasing) between members of a colony include burrow defense by breeding females, nonreproductive females chasing yearlings, and yearlings chasing yearlings (Taulman 1990a,

1990b). An *M. caligata* that intrudes into another colony is chased by the 1st adult that detects its presence (Taulman 1990a, 1990b).

Reproductive behavior.—Mounting, but not copulation, has been observed directly. Mounting occurs between and within sexes (males and females; females and females) and age groups, although not between yearlings or young (Barash 1974; Taulman 1975). Individuals initiate mountings with greeting or sniffing of the anogenital region (Barash 1974; Gray 1967; Taulman 1975). During mounting, the individual on the bottom arches its tail and holds it to the side or flat along the back, and the individual on the top grasps the fur of the neck with its teeth (Barash 1974; Taulman 1975).

Females provide direct parental care to infants in the natal burrow (Holmes 1984a), but after appearing aboveground, only indirect parental care (social interactions, construction and protection of colony resources, and warnings) is provided to young of the year (Gray 1967; Holmes 1984a). Maternal behavior (time spent near an infant and number of infant greetings) is similar for females in an “isolated” town (1 adult male) or a “colony” town (3 adult males). Paternal behavior, however, varies by colony type. Males in isolated towns exhibit greater parental behavior (burrow sharing, time spent near an infant, and number of infant greetings) and decreased levels of social interactions with individuals outside the family unit than those in colony towns (Barash 1975a, 1989).

Young exhibit the following behaviors in the first 4 weeks aboveground (Gray 1967; Taulman 1975): at 1st emergence young are wary, startled by movement, sounds, alarm calls, and other animals and run to burrow; on days 1–3, they feed on grass and experiment with food types, play, greet and groom each other, and show mouth-wiping behavior; by end of 1st week, young are less wary, show complete or partial adult behaviors including increased mutual contact and play, vocalizations, carrying and moving rocks, and running with tails arched; tail flipping behavior may (Taulman 1975) or may not (Gray 1967) be exhibited at this time; by 2 weeks, exploratory behavior decreases; by 3 weeks, young gather grass and interact with adults; at 4 weeks, young feed throughout colony, display frequent interactions with adults, and play and wrestling are common.

Communication.—*Marmota caligata* exhibits 7 distinct vocalizations (Taulman 1977): long calls, descending calls, ascending calls, low-frequency calls, growls, whining, and tooth chattering. Gray (1967) described a long- and short-interval whistle, accelerando whistle, flight whistle, short alert whistle, “que-uck” whistle, and yelp. Four structurally distinct alarm calls (ascending, flat, descending, and multiple-note trills) were described by Blumstein (1999). Long calls or “whistles” have a duration of 0.56 to 0.74 s (Taulman 1977; Waring 1966), a harmonic, and a frequency of 3,200 Hz; call frequency ranges from 2 to 7.6 calls/min

with a mean of 4.4. Descending calls have a duration time of 0.3 to 0.5 s, a frequency of 3,500 Hz, and may be given every 3 s. Ascending or medium calls include chirps and accelerating chirps that differ in duration and intercall interval. Ascending calls begin at 2,000 Hz and ascend to 3,200 Hz; call duration is 0.25 s. Chirps are initiated by a burst of air from the vocal chords, have a duration of 0.1 s, and an interchirp interval time of 1.3 s. Accelerating chirps include an ascending chirp, a pause, followed by 5–7 accelerating chirps with decreasing duration and interchirp interval. Low-frequency calls have a duration of 0.3 s and a frequency between 1,000 and 3,000 Hz; the call ascends quickly followed by a gradual decrease in pitch. Growls may be steady (continuous) or barking (short). Whining has a frequency of 300 to 900 Hz. Tooth chattering is known only for marmots in captivity.

Long or alarm calls generally serve as a warning when an aerial or terrestrial predator is sighted, but also are given in response to the presence of nonpredators (Blumstein 1999; Holmes 1984a; Noyes and Holmes 1979; Taulman 1975, 1977, 1990b; Tyser 1980). Whining occurs in response to growls from other *M. caligata*. *M. caligata* responds to calls by becoming alert and visually tracking the area or running to a refuge and visually tracking the area (Noyes and Holmes 1979; Taulman 1977); calls often are given after reaching a refuge (Noyes and Holmes 1979). Calling among age classes is not significantly different; however, for adults and their juveniles, adults are 1st callers significantly more often than juveniles, although difference between dams and sires is not significant (Holmes 1984a).

Alarm communication in 8 species of marmots, including *M. caligata*, was studied by Blumstein (2007). The acoustic adaptation hypothesis (a call is best transmitted in its own habitat) was tested and falsified; variation in alarm call microstructure may be explained by drift rather than selection from the habitat. Repertoire size (number of types of alarm calls) was not related significantly to home range size or transmission fidelity, but 57–59% of variation in alarm call repertoire was explained by social complexity. Although the microstructure of alarm calls exhibited some variation as a function of stimulus type (aerial or terrestrial) and distance to the stimulus, *M. caligata* did not have unique responses to alarm call types or unique stimulus-class-specific vocalizations (Blumstein 1999).

Alert behaviors include “look-up,” “upright-alert,” and “sunning-lookout” (Barash 1989; Noyes and Holmes 1979; Tyser 1980). Look-up (pausing while feeding) and upright-alert (sitting up and visually scanning the area) behavior is exhibited when foraging in meadows, and sunning-lookout (boulders used as vantage points) behavior generally occurs on boulders ≥ 2 m in diameter in both meadows and talus. Number of look-ups per minute and feeding time per minute varied significantly across age classes (Holmes 1984b). Alert behavior is correlated with risk; individuals looked up more

often and spent less time feeding when young, feeding alone, and foraging far from talus (high risk) compared with older *M. caligata*, animals feeding near other individuals, and foraging near to talus (low risk).

Scent marking is used by male and female *M. caligata* to define the colony territory, mark refuge burrows, express dominance over another individual, and communicate identity (Taulman 1990a). Rocks, mounds, dirt, and grass are marked by rubbing the cheek with an upward motion of the head or by placing the shoulder on the ground and rubbing the cheek on the surface (Gray 1967; Taulman 1990a). Defecation occurs widely throughout the colony, including on burrow entrance mounds, trails between burrows, and meadows (Gray 1967; Taulman 1975). Some burrows or burrow parts, however, may be used for defecation and urination on the basis of the presence of strong odors and scarab beetles (Gray 1967). *M. caligata* exhibits a stereotyped defecation behavior; at 1st emergence in the morning marmots defecate on or over the edge while facing the burrow (Taulman 1975).

Miscellaneous behavior.—The activity pattern of *M. caligata* varies seasonally (Barash 1973, 1989; Gray 1967; Taulman 1975, 1990b) and is correlated with daily temperatures (Gray 1967). In early spring and late summer, it is unimodal with a peak at midday; in midsummer, it is bimodal with peaks in the morning and late afternoon with a decline of activity at midday (Barash 1973, 1989; Taulman 1975, 1990b). By mid-September, time above ground decreases and the period of inactivity at midday is absent (Taulman 1975, 1990b). Activity is not affected by weather conditions other than temperature and extreme weather (Gray 1967; Taulman 1975).

Typical daily activity is emergence from burrows in the morning and foraging during the day; periods of inactivity are spent in sleeping burrows or refuge burrows in meadows (Barash 1989; Gray 1967; Taulman 1990b). Most time above ground is spent in meadows (74%) foraging (84% of time in meadows) or in other nonalert behaviors (Karels et al. 2004b; Tyser 1980). Less aboveground time is spent on bare ground or on talus (25%, Gray 1967; 26%, Karels et al. 2004b) or in look-up (11%) or sunning-lookout (18%) behaviors (Tyser 1980). As summer proceeds, activity and foraging time decrease (Barash 1989); from August to September, foraging time decreases 50% (adults and yearlings) and 60% (juveniles) and time spent resting increases 129% (adults and yearlings) and 467% (juveniles—Taulman 1990b). *M. caligata* will sit at burrow entrances after emergence in the morning and before and after activity periods (Barash 1989; Gray 1967), often using the ground or rocks for sunning (Bailey 1918; Barash 1989; Gray 1967; Howell 1915; Tyser 1980). Percent aboveground time in the morning spent sunning is 44% on clear days, but < 10% on cloudy days (Barash 1989). At temperatures > 20°C, individuals enter burrows or lie in the shade of boulders (Gray 1967).

Time spent foraging by reproductive and nonreproductive females is not significantly different; however, in early summer, reproductive females foraged more during the evening and in poor weather conditions (Barash 1980, 1989), and at a greater distance from the nearest burrow and talus (Barash 1980, 1989; Holmes 1984a). Foraging activity decreases before hibernation (Barash 1976). Adult males and adult nonmaternal females terminated aboveground activity earliest (by late September–early October), followed by yearlings (by mid-October), and last, adult maternal females and infants (late October—Barash 1976, 1989). The pattern is consistent for a species with high winter mortality, high juvenile mortality, lack of feeding during the winter, and a short growing season. Because weight is not regained until after weaning, maternal females must replace metabolic losses before hibernation (Barash 1976, 1989). The hibernation period is 8 months and extends from immittance in September to emergence in early to mid-May (Barash 1989; Gray 1967; Hock and Cottini 1966; Holmes 1984a). In mid-May, *M. caligata* emerges to the surface by digging through the snow (Gray 1967); existing burrows are excavated by digging through the snow to expose the openings (Barash 1989).

Marmota caligata feeds selectively among plant species and crop vegetation faster than it is regenerated (Holmes 1984b). Shifting of feeding between years to different patches in a colony is related to food abundance, refuge burrow density, and distance from sleeping burrows (Holmes 1984b). Foraging activity (% time feeding or gathering food) is related to seasonal changes in plants and nutrient value (Barash 1973); it is lowest in early June (about 15%), highest in July (about 40%), and decreases through mid-August (about 20%). Most foraging time (85%) occurs within the colony home range (Holmes 1979) and is > 90% for females (Holmes 1984a). Foraging distance is related to age and foraging time (Holmes 1984b). Mean foraging distance from home talus is reported as 11.6 m (Karels et al. 2004b) and 49.9 m (Barash 1973; Holmes 1984b). Adults foraged at greater distances (\bar{X} = 52.1 m) than 2-year-olds (\bar{X} = 43.4 m) and yearlings (\bar{X} = 32.2 m—Holmes 1984b). Foraging trips averaged 214 s (24 to 1,100 s—Barash 1973) and foraging time was greater for individuals feeding near talus (Holmes 1984b). Forage patches enhanced with ammonium nitrate had greater use by all age groups (625% increase in total foraging time—Barash 1989; Holmes 1984a, 1984b). *M. caligata* forages by moving slowly through the colony (Gray 1967; Taulman 1975), but also will feed insatiably in 1 place (Taulman 1990b) and lying down (Gray 1967). “Crop-search” food gathering accounted for 96.8% of aboveground time (Tyser and Moermond 1983).

Social grooming accounts for < 1% of activity and occurs among all age classes during rest periods (Taulman 1975). Individual grooming is more common at midday and before hibernation (Gray 1967). Grooming postures include

lying, sitting, sitting up (= on haunches), standing, and stretching and yawning generally while sitting, lying, or basking on a rock or entrance mound (Gray 1967; Taulman 1975) and less frequently while foraging or traveling (Taulman 1975).

Locomotion includes 4 types: normal walking—used when moving between burrows and feeding areas and crossing bare ground or snow; slow, irregular walking—used when feeding and moving short distances; galloping—the normal gait and used when moving a long distance; and running—used in chases, running from predators, and when responding to alarm calls (Gray 1967; Taulman 1975). Tail-flipping behavior (flipping tail over the back) is associated with the first 3 types of locomotion and serves in visual communication (Gray 1967). Young of year run, but do not gallop (Gray 1967). *M. caligata* is a good climber and has been seen on cliff faces (Bailey 1918) and jumping into trees from snowbanks (Gray 1967).

Marmota caligata occasionally responds to calls by Columbian ground squirrels, but not to calls by the American pika (Tyser 1980); both species, as well as the collared pika, however, respond to alarm calls by *M. caligata* (Trefry and Hik 2009; Tyser 1980). Columbian ground squirrels retreat from *M. caligata* during agonistic encounters (Tyser and Moermond 1983). Although birds, except raptors, were generally ignored, young of the year chased magpies (*Pica pica*—Gray 1967) and kestrels (Taulman 1975, 1990b). When encountering humans away from rock piles, *M. caligata* often runs for the nearest available refuge (Dixon 1938). In some areas (e.g., Glacier National Park—Lechleitner 1955), *M. caligata* may become habituated to the presence of humans.

GENETICS

The diploid number (2n) in *Marmota caligata* is 42 chromosomes and the fundamental number (FN) is 62. Autosomal pairs consist of 1 large metacentric, 1 small metacentric, 9 submetacentric, and 9 acrocentric chromosomes. The X chromosome is large and submetacentric and the Y chromosome is minute and dotlike in structure (Hoffmann and Nadler 1968; Rausch and Rausch 1965, 1971). Karyotypes of *M. caligata caligata* and *M. caligata nivaria* [= *okanagana*] are identical (Hoffmann and Nadler 1968). Morphologically, the autosomes of *M. caligata* are indistinguishable from those of the Vancouver Island marmot and the yellow-bellied marmot; the X chromosomes are submetacentric in *M. caligata* and the Vancouver Island marmot and are metacentric in the yellow-bellied marmot (Rausch and Rausch 1971).

Genetic variation among individuals of *M. caligata* was assessed by Hoffmann et al. (1979). Among 3 blood serum proteins, albumin and leucine aminopeptidase were monomorphic, and transferrin was polymorphic. Seven microsat-

ellite loci developed from *M. caligata* were polymorphic, with a range of 2–7 alleles/locus (Kyle et al. 2004). Of 13 microsatellite loci developed for *M. marmota* (alpine marmot), *Spermophilus citellus* (European ground squirrel), and the Columbian ground squirrel, all were polymorphic with 2–9 alleles/locus (Kyle et al. 2004). Primer sequences for the microsatellite loci are registered with GenBank (AY702707, AY702708, AY702709, AY702710, AY702711, and AY702712; Kyle et al. 2004).

On the basis of the mitochondrial cytochrome *b* gene, *M. caligata* is part of a clade of western North American species of *Marmota* (Kruckenhauser et al. 1999; Steppan et al. 1999); results on the basis of the shape of the lower 3rd molar are similar (Polly 2003). The clade of yellow-bellied marmot–Olympic marmot–Vancouver Island marmot + *M. caligata* (Steppan et al. 1999) or yellow-bellied marmot (*M. caligata* [Olympic marmot + Vancouver Island marmot—Kruckenhauser et al. 1999]) is basal and sister to a clade of other species of Holarctic *Marmota*. Molecular (Brandler and Lyapunova 2009; Steppan et al. 1999) and cytogenetic (Rausch and Rausch 1965, 1971) data support the recognition of the Alaska marmot, which was described as a subspecies of *M. caligata* (Hall and Gilmore 1934), as a distinct species not closely related to *M. caligata*. The complete cytochrome *b* gene (mitochondrial genes and nuclear pseudogenes) is sequenced in *M. caligata* and is registered with GenBank under the following accession numbers: AF100718, AF100722, and AF143920 (Kruckenhauser et al. 1999; Steppan et al. 1999).

Microsatellite molecular data determined or corroborated field-assigned maternity and paternity for 83% of litters (Kyle et al. 2007). Genetic data revealed cryptic relationships such as reproductive success of subordinate males and males not regarded as dominant, and cuckoldry (Kyle et al. 2007).

CONSERVATION

Marmota caligata maintains a stable population trend and is considered a species of “Least Concern” by the International Union for Conservation of Nature and Natural Resources (2008). Cook (1998) and the State of Alaska (Alaska Department of Fish and Game 2006) recognize *M. c. sheldoni* (Montague Island hoary marmot) and *M. c. vigilis* (Glacier Bay hoary marmot) as distinct subspecies rather than synonyms of *M. c. caligata* and consider them to be of conservation concern. Conservation problems and issues, habitat concerns, conservation objectives and actions, and determination of taxonomic status for both taxa were outlined by Cook (1998) and in the Alaska Comprehensive Wildlife Conservation Strategy (Alaska Department of Fish and Game 2006). Both taxa were reported as abundant (less so on the islands in Prince William Sound; Heller 1909, 1910) when the original

collections were made; however, neither taxon has been documented since the early 1900s, although observations of marmots on the west side of Glacier Bay (“observed recently,” Cook 1998) and on Montague Island (in 1978; Lance 2002) have been reported. Logging, road construction, and species introductions (e.g., *Odocoileus hemionus*—mule deer and *Neovison vison*—American mink) may affect populations of *M. caligata* on Montague Island through habitat loss and fragmentation as has been reported for the Vancouver Island marmot (Bryant 1996; Bryant and Janz 1996; Cook 1998; Lance 2002). Introductions of *M. caligata* to Prince of Wales Island (1930 and 1931) failed (Paul 2009); however, marmots introduced to Sud Island (1930), possibly by the military during World War II during its use of the island as a communications outpost, were numerous in 1974 (Bailey 1976).

Marmota caligata is managed by the Alaska Department of Fish and Game as a furbearer; there is no closed season or bag limit (Alaska Board of Game 2008). There are no known negative impacts associated with *M. caligata* and no known economic uses. Although pelts identified specifically as *M. caligata* were never exported by the Hudson’s Bay Company (MacFarlane 1905), fur trade documents indicate that “marmots” were traded beginning in 1856 (Nagorsen et al. 1996). *M. caligata* was used as a food source for Native Americans (Dixon 1938; Howell 1915; King 1836; Richardson 1829) and the hides were utilized in making clothing (Armitage 2003; Drucker 1950; Dufresne 1946; Howell 1915; King 1836; MacFarlane 1905), robes (Dixon 1938; MacFarlane 1905), bedding (Dixon 1938), and blankets (Richardson 1829). Hides were used in potlatch ceremonies and as a form of currency and wealth among the Tlingit and Gitksan tribes (Armitage 2003; Drucker 1950). Four tribal groups (Nootka, Kwakiutl, Tsimshian, and Tlingit) of the Pacific Northwest hunt *M. caligata* in the autumn after molting and before hibernation (Drucker 1950). September is known as the “digging moon” by the Tlingit (de Laguna 1972) and the “marmot hunting moon” by the Gitksan (Drucker 1950). The Kwakiutl, Tsimshian, and Tlingit place deadfall traps in front of dens and the Tlingit also incorporate special carved triggers that resemble the human figure. The Sanyakwan and Chilkat of the Tlingit tribal group sang special songs during the preparation of marmots, although each practiced variations of specific hunting and preparation observances. *M. caligata* has been maintained in captivity or as pets although “they are difficult to tame, but when attached, become playful and are fond of being handled...neglect or long absence, however, soon renders them again wild and unmanageable” (King 1836:243).

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